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BIOMETRIC EVIDENCE IN THE PROBLEM OF THE PAIRED LIMBS OF THE VERTEBRATES.

BASHFORD DEAN.

FROM early development onward a fish is accurately poised in its living medium. Its long axis in a position of rest remains normally horizontal, in spite of the most varied changes in the size and shape of the fish's body and the shiftings and differentiation of its component parts. To preserve an accurate balance under conditions of rest as well as under the strain of the most active movement implies obviously a delicate adjustment of the morphological elements of the animal to the physical ones. And as the latter are relatively constant it follows that the acute strain in the evolution of the fish's body, both in ontogeny and phylogeny, has fallen upon the morphological elements. These, then, become subject to form changes, to position changes, and, most important, to physiological changes, to enable them to fulfill the mechanical requirements of habitat. To what degree the results are successful in adapting the vertebrate body to aquatic living can best be understood by comparison of the "area curves" and "entering

angles," not only among fishes of different groups but between fishes and cetaceans; for in these practically the same "lines" and "entering angles"¹ obtain.

From a physical standpoint we conclude, therefore, that the position of the gravity center of the animal during different stages of growth plays an important rôle in connection with its ever-increasing body length, and that special organs of balancing, *i.e.*, fins, will in their development be subject *par excellence* to the mechanical needs in shifting which the changing position of the gravity center and increasing body length demand.

From this standpoint, then, one can attack the long-troubled problem of the origin of the vertebrate limbs. Not, however, with the aim of solving it indisputably, — for this I firmly believe can be done only by the paleontologist, — but rather for the purpose of finding a probable clue to the labyrinthine confusion in latest morphological studies; for the voluminous conclusions of Braus, following Gegenbaurian teachings, and supported by Semon in his recent work on *Ceratodus*, — *cf.* also the related work of Klaatsch, — are vigorously denied by the newer phases of the fin-fold theory of Dohrn, Mollier, Rabl, and others, which in turn are in the latest time criticised by Fürbringer. In short, there is at present a deadlock in the discussion as to the mode of origin of the limbs of the vertebrates which cannot yet be loosened by orthodox embryological methods. Perhaps it will be bettered when a greater number of forms will have been examined, or when we shall have a clearer knowledge of the processes of accelerated and retarded development. Perhaps, on the other hand, to take a more somber view, it will never be adequately loosened by study of embryonic structures, since these may have been so modified during phylogeny as to mask hopelessly their true homologies. For the discussion has to a large measure narrowed itself down to the interpretation of embryological details, which if given fixed morphological weight become of great importance in theoretical discussion, but which are relatively valueless if

¹ The entering angle terminates with "wonderful uniformity" at 36 per cent of the total length of the animal, whether teleost or cetacean. *Cf.* especially H. DeB. Parsons, *Trans. Amer. Soc. Engineers*, vol. ix, 1888. 17 pp., 7 pls.

viewed as nothing more than adaptations to recent physiological needs. Thus, as an example, a tangle of nerves and blood vessels on the tailward side of a fin lobe of a shark may be either an important morphological condition as vestige of an ancestral, paddle-shaped, ceratodont fin, *e.g.*, as Braus maintains, or it may be nothing more than a newly developed condition to enable muscles and nerves to get in better touch with an enlarging and specializing margin of the fin, — which may indeed in its growth be developing from stage to stage special embryonic and larval movements. Again, the emancipation of nerves, vessels, and muscles from the basis of an embryonic fin may be the result either of the migration of a gill bar element in the Gegenbaurian sense, or merely of a purely local change in the requirements for balancing the constantly growing animal. For the center of gravity may shift as the body grows, and the fin (in sharks functional even when the “larva” is growing within the egg case) may thus have to move forward and backward as mechanical needs demand.

“But,” the Gegenbaurian would maintain, “*our* theory is supported by fin migration. Of course we are willing to grant that the record is obscured by cenogenesis, but we have still morphological evidence that the ventral fin migrates backward, and that the pectoral is relatively stationary, its girdle resembling the adjacent branchial arches. And we believe, moreover, that the mechanical fin needs, which have been noted above, are of the utmost importance, since it is in response to them that the ventral fin has traveled backward and that the pectoral fin has retained, relatively, its primitive position. Indeed, the very perfect segmental character of the ventral fin can be best explained in terms of a continued hindward migration, for the ventral is not the more steadfast and more primitive fin.”

Now, it has long seemed to me that such a line of argument could be invalidated if it could be shown that during the growth of the individual the fins responded to their mechanical requirements in just the opposite way ; that is, that the ventral fin was *not*, and that the pectoral fin *was*, the migrating element. And the present paper has grown out of an attempt to trace,

and to this end by biometric methods, the actual stages in the development of the paired fins in accordance with their physical requirements. Assuming, for example, a complete series of a form in which the limb characters can be favorably examined, say a shark,¹ in stages ranging from adult to embryos in which the paired limbs are just appearing as distinct structures, we can then determine by measurement what change occurs from stage to stage in the position of the gravity center (with reference to the total length of the animal), and by similar measurement of the fins in similar terms we can ascertain what ratio these measurements bear to the possible shifting of this center. For all will admit that the fins themselves, as light and delicate structures, can in their growth play little direct part as a *cause* of the changing position of the center of gravity, and that their migration, forward or backward, is rather an outcome of the shifting of bulkier organs, — muscles, brain, viscera, sense organs. We can therefore conclude that by such a system of measurements one can obtain evidence as to whether the ventral fins migrate backward, *i.e.*, in terms of the total length of the individual, and show the correlation in growth with the pectorals which the Gegenbaurian theory demands; or whether, on the other hand, it is the ventrals which are constant, and resemble the dorsal fins, while pectorals play the part of the mobile and specializing members.

The following notes are based upon a cestracient shark,² a form particularly interesting from the standpoint of morphological conservatism, since there is reason to believe that it has been little modified since Carboniferous times. And the measurements are recorded of sixty individuals ranging in length from 330 mm. to 14.5 mm. For this careful and laborious computation I am much indebted to my former student, Prof. C. H. Brookover, who made it the beginning of a research

¹ Better, of course, would be sets of many genera and species; but as long as these are lacking, we may base conclusions as to essential characters upon the ontogeny of a single form.

² *Heterodontus japonicus* Macleay. The embryos were collected during the writer's visit to Japan, 1901, thanks to the many privileges which he enjoyed at Misaki as guest of the Imperial University of Tokyo.

upon the general problem of limb migration. He was, however, unable to carry out his plans, and he generously turned over to me his measurements for use in the present paper.

DETAILS OF DATA.

Straight specimens were selected for measurement. Gravity center was determined in terms of the total length¹ by balancing the specimen either on a knife-edge or within the delicate tips of curved forceps. By this simple method the limit of error was found to be surprisingly small, estimated by repeated tests at about 1 per cent. In the measurements individual variations are taken into account, since it was found that a more advanced embryo is sometimes smaller in size and variable slightly in proportions, and in preparing the table of averages as plotted in Fig. 1 this source of error has been largely counterbalanced by the use of guide points representing the average of several (usually four) successive individuals. All measurements are computed in percentage of the total length of the specimen, and are estimated from the snout tip. The landmarks whose relative position is computed are indicated graphically in the present Fig. 1, *i.e.*, anterior margins of pectoral, of ventral, and of dorsal fins, and posterior margins of pectorals and ventrals. Of the latter margin the functional (dermal) one is alone considered.

THE RESULT OF THIS ANALYSIS.

The *center of gravity* is found to shift forward (about 5 per cent of the total length) in the earlier embryos (embryos from 27 mm. to about 6 mm.), in later stages (up to embryos of 200 mm.) backward to the extent of about 8 per cent of the total length. In well-grown specimens the position of the gravity center remains practically unchanged.

The *pectoral fin* undergoes conspicuous changes: from the time it can be distinctly differentiated from the ventrals it

¹ The transverse plane in which the center occurs was alone determined; its more accurate position *within this plane* has evidently no bearing upon the present problem.

TABULATED MEASUREMENTS OF FINS AND GRAVITY CENTER
OF CESTRACION EMBRYOS.

(By C. H. BROOKOVER.)

	TOTAL LENGTH.	FROM SNOUT TIP TO						
		CENTER GRAVITY.	ANT. MARG. PECT. FIN.	POST. MARG. PECT. FIN.	ANT. MARG. VENT. FIN.	POST. MARG. VENT. FIN.	FIRST DORSAL.	SECOND DORSAL.
	<i>mm.</i>	<i>%</i>	<i>%</i>	<i>%</i>	<i>%</i>	<i>%</i>	<i>%</i>	<i>%</i>
1	14.5	—	31 +	38 —	—	—	—	—
2	15	—	32	40	—	—	—	—
3	15	—	27	35 —	—	—	—	—
4	20.5	—	26	38 +	42 +	49 +	no spine 39	no spine 63 —
5	21.5	—	25 —	32 +	41 —	48 +	37 + no spine	56 —
6	24 —	—	24 +	31 —	37 +	44 —	35 +	58 +
7	24	—	28 —	37 —	45 —	52 —	40 —	62 +
8	26.5	—	26 +	32 +	40 +	48 —	33 —	53 —
9	26.5	31	27 —	33 —	41 +	48 +	34	57
10	27	28	24 +	30	37	44 +	34 —	53
11	27	26 —	25 —	31 —	39 —	45 +	33	53
12	27.5	—	24 +	31 +	38 +	46 —	32	57
13	28	—	21	28	32	39	30 bent	50 bent
14	31	—	23	31	39	45	32	55
15	31	—	25	31	37	43	32	50
16	32.5	—	24	30	38	41	29	50
17	34	—	22	28	34	40	31	50
18	34.5	—	22	29	34	40	28	49
19	35	—	24	31	38	45	30	51
20	35	—	20	26	30	38	29	48
21	35	—	22	28	34	40	29	50
22	37.5	—	23	29	31	45	29	50
23	38	—	22	28	39	46	30	50
24	39	—	22	29	39	44	29	51
25	39	—	21	27	35	43	27	50
26	39	—	21	27	34	40	27	48
27	40	—	20	26	32	40	28	48
28	40	—	21	29	36	42	28	50
29	40	26	21	27	35	41	27	48
30	40.5	—	20	26	35	40	28	48
31	41	—	22	27	35	43	26	47
32	41	—	21	29	34	41	29	50
33	41.5	—	20	26	30	39	26	47
34	42.5	—	22	28	36	42	28	50
35	43	—	22	29	39	44	29	49
36	43	26	21	26	34	40	25	45
37	44.5	26	20	26	34	39	29	50
38	44.5	—	21	27	37	43	27	49
39	45	—	22	27	36	43	27	48
40	46	—	20	26	34	38	27	48
41	46.5	31	22	27	35	42	27	48
42	50	25	20	26	37	41	27	46
43	50	24	21	25	32	38	24	43
44	50	25	20	26	33	40	25	47
45	51	—	20	26	33	40	25	50
46	55	25	19	25	35	41	26	46
47	59.5	24	18	24	31	39	23	50
48	60	23	21	27	34	40	25	47
49	61	25	18	25	34	41	25	48
50	62	23	19	26	34	41	27	47
51	66	26	19	23	33	40	24	46
52	72	25	17	26	33	41	24	51
53	73	26	18	30	37	42	27	50
54	81	25	19	29	30	43	26	52
55	82	24	19	30	37	43	27	52
56	105	27	19	30	37	46	27	53
57	187	31	17	42	37	50	27	57
58	197	32	18	42	41	53	30	57
59	280	30	18	39	41	53	31	59
60	330	30	18	43	41	53	29	59

increases greatly in size, measured antero-posteriorly, from 6 per cent of length to about 24 per cent, its anterior and posterior margins undergoing somewhat different fates. The anterior rim of the fin passes forward, suddenly in earlier stages, slowly in later ones, altogether a distance of over 12 per cent of the total length, a distance considerable enough, I take it, to entail important adaptive changes in the structures of the encroached-upon region, especially in view of the fact that this fin margin grows forward as the gravity center passes backward. (*Cf.* also *infra*, *re* the continuous hindward growth of the outer gill slits.) Interesting in this connection is the slight variant in embryos of about 80 mm.; here, the gravity center shifting a little forward, the anterior fin margin passes backward, thus indicating a nice adjustment in the mechanical relations between them. In a general way the advance of the anterior rim of the pectoral is at the same pace as the retreat of the center of gravity. The behavior of the hinder rim of the pectoral shows a less close adjustment to the gravity center. In early stages this fin rim passes forward (about 11 per cent between stages of 15 mm. to 56 mm.) to about the transverse plane of the center of gravity; thereafter, however, it grows hindward, gradually increasing the distance from the gravity center (11 per cent) (and from the anterior fin rim (total, 24 per cent)). By this noteworthy hindward growth it comes in the older stages to overlap somewhat the anterior rim of the ventral fin.

The *ventral fin* is conservative in its position during growth: measuring about 6 per cent of the total length in earlier stages, it increases to but 12 per cent in latest ones, a gain in percentage of but 6 per cent as against 18 per cent in the pectoral. Like the pectoral, the entire fin passes slightly forward in younger stages, then slightly backward. The anterior rim remains almost fixed with reference to the body length, the posterior passing slightly backward to a degree corresponding almost exactly with the shifting of the gravity center. Thus, in an embryo of about 80 mm. the center of gravity is 18 per cent in advance of this rim, in one of 115 mm. 19 per cent, in one of 145 mm. 19 per cent, of 187 mm. 19 per cent, a

correspondence so close that we can interpret it only in terms of cause and effect.

The *dorsal fins* are even more conservative in position than the ventrals. In the first place they maintain practically the same relative distance from one another, measured from the anterior rim of the fins¹: thus, in a specimen of 21 mm. the interval measures about 23 per cent, of 40 mm. about 22 per cent, of 60 mm. 23 per cent, of 82 mm. 25 per cent, of 105 mm. 26 per cent, of 197 mm. 27 per cent; in other words, between the two fins there is but a slight variation in the interval (say, 5 per cent of the entire length) in stages widely different in size (*e.g.*, measuring between 20 and 200 mm.). In general, however, we note that the growth of the anterior rims of first dorsal and ventral are indicated by parallel lines, and similarly the growth of the anterior rim of the second dorsal and the posterior rim of the ventral.

SUMMARY.

The foregoing characters yield what seems to me convincing evidence that the pectoral fin is subject to changes with respect to the gravity center, *i.e.*, physical changes, which cause it to become more highly specialized than the ventral fin, and that the latter is conservative, after the fashion of the unpaired fins. The result of biometric data, it will be seen, confirms strikingly the views of the fin-fold theorists, most clearly expressed in this particular regard by Wiedersheim in his "Gliedermassenskelet." On the other hand, the present study yields *no evidence that there has ever been a migration of the fins in the Gegenbaurian sense*; thus, we find no reason to believe that the ventral fin is a structure which has shifted its position from in front hindward; it is indeed in about the same position fore and aft in the adult as in early embryos (20 mm.). It is important, furthermore, that the only fin (leaving anal and caudal out of discussion) whose anterior margin passes forward is the pectoral, since with this condition is correlated the fact that this

¹ In the younger stages the measurement was made from the actual most anterior point of the fin; in the later, when a spine appears, from the point where the anterior fin rim, if produced, would intersect the dorsal-most line of the body.

rim alone is in advance of the gravity center. Thus, as this center passes backward, the posterior margin of the ventral fin is found to follow it *pari passu*, and, as effecting a counter balance, like equal weights placed in opposite scale pans, the anterior rim of the pectoral passes headward.

Again, contrasting the embryos shown drawn to scale in Fig. 1, and referring now to the position of the external gill openings, we note that there is a marked tendency for these openings to pass backward. In the earlier specimens all are widely interspaced and the last is well in front of the fore rim of the pectoral; in the next embryo the openings are drawn together, altogether somewhat tailward; and in the latest, as far at least as to the second opening, the series have taken a position hindward of the rim of the pectoral.

More concretely (measurements taken from the specimens):

GILL OPENING.	PERCENTAGE OF LENGTH FROM SNOUT TIP.			PERCENTAGE OF TAIL- WARD MIGRATION.
	<i>Stage 1.</i>	<i>Stage 2.</i>	<i>Stage 3.</i>	
I	11 %	13 %	16 %	5 %
V	19 %	19 %	23.5 %	4.5 %

In other words, as far as these openings are concerned, and with them the *outer part* at least of the gill canal, it is evident that in the older stages a definite migration has taken place, to a degree that, in terms of the total length of the animal, the gill openings come to occupy a position in the body wall which is largely behind that of the earlier stages. Numerically considered, the interval between gill openings I and V is about 8 per cent of total length in stages 1 and 3; but in the latter the region of the gill openings is nearly 5 per cent farther tailward; therefore, in this stage the openings occupy a position in the body surface which is about five-eighths new, *i.e.*, never before occupied by gills. From this it follows that *the gill region, at least in its outer part, shows no affinity during proportional growth with the neighboring region of the pectoral fin. In fact, from an early stage onward, they are evidently growing in opposite directions.*

If, now, we figure the matter up, we find that the distance the gill openings pass tailward (contrasting embryos varying from about 20 to 300 mm.), added to the distance which the anterior rim of the pectoral passes headward, makes the considerable sum of 20 per cent of the length of the animal. And from this it follows that there occurs in this region a process of "shortening up," which is surely enough to account for the presence of anastomosing vessels, blended muscle bands, plexus of nerves, and "collectors." The presence of such complicated structures,¹ especially in the region of the anterior or posterior rim of a (pectoral) fin, is therefore to no little degree a product of the mechanical needs of fin migration.

COLUMBIA UNIVERSITY, October 17, 1902.

¹ Another complicating feature to be considered in this connection is the disposition of segments arising in the caudal region and growing cephalad. In the earlier embryos (15 to 20 mm.) the total number of segments behind the last gill arch is enclosed within a space measuring about 80 per cent of the entire length; later specimens (300 mm.) include the segments within a space of 76 per cent. The size of the embryo at which the formation of new segments ceases has not been determined in the present form, nor is it as yet ascertained in kindred forms.

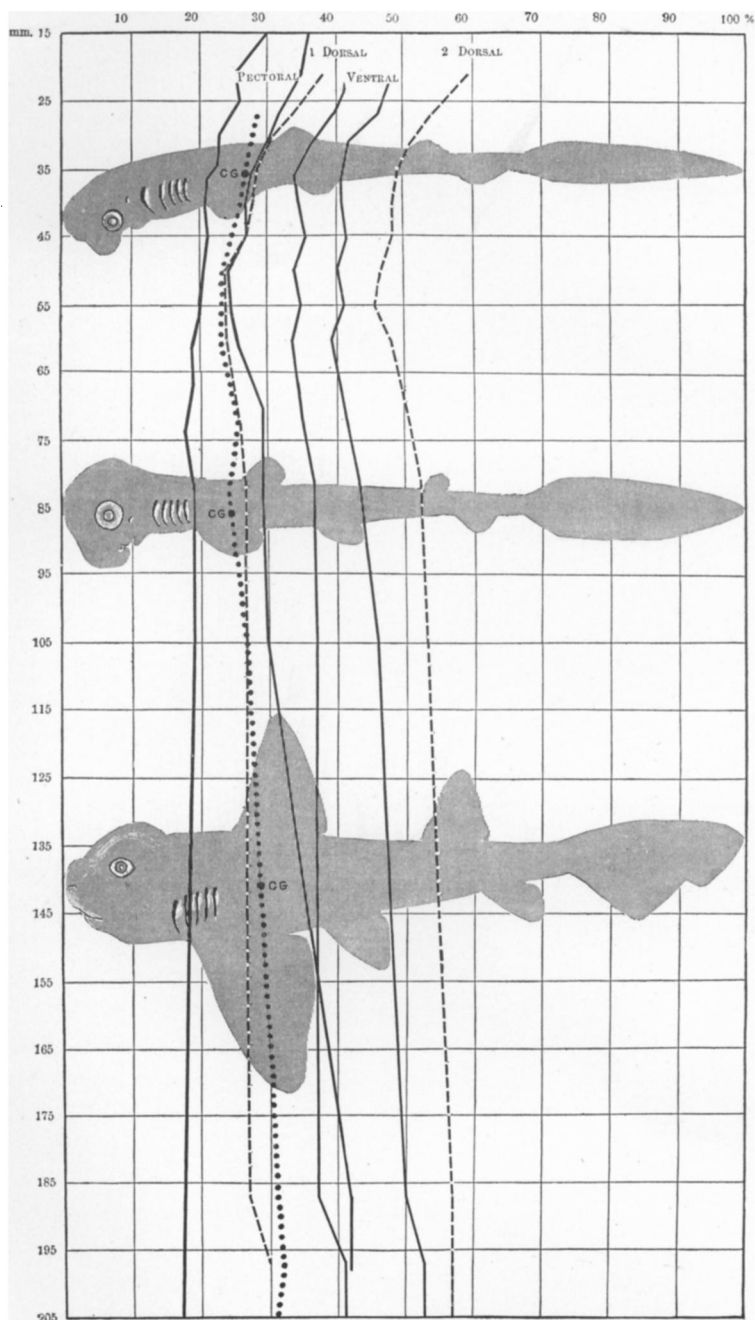


FIG. 1.—Cestracion at different growth stages. Tabulated measurements of sixty specimens indicating the position of the center of gravity and of the paired dorsal fins. In all specimens in the series the measurements are reduced to a common scale, *i.e.*, to a uniform length, which is here subdivided in percentage. The lengths of the specimens measured are indicated (in millimeters) in the vertical columns at the left. The landmarks in the different stages measured are connected by lines as follows: gravity centers, *CG*, by dots; fin margins of pectoral by heavy lines; of ventral by light lines; of dorsals by dashes. Outlines of stages of 35, 85, and 138 mm. are introduced to show these lines in their relative positions.